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Winter habitats of Atlantic salmon, brook trout, brown trout and rainbow trout

A literature review

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<p>A review of winter habitat studies in ice-covered streams for four species of salmonid (Atlantic salmon, brook trout, brown trout and rainbow trout) provided some general information on substrate conditions and focal point velocities and depths. All species of fry are found at depths less than 40 cm and at velocities of 10 cm/s or less; juveniles of all species are found at velocities of less than 15 cm/s. A lack of continuous physical, chemical and biological measurements throughout the ice-covered season was a common deficiency of the studies reviewed. The interaction of the ice cover with other physical processes in the stream was rarely addressed. <i>Key words:</i> Salmonidae, Salmoniformes, Marine Biology, Ecology, Habitats, Fishes. (AW)</p>					
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PREFACE

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Winter Habitats of Atlantic Salmon, Brook Trout, Brown Trout and Rainbow Trout A Literature Review

DARRYL J. CALKINS

INTRODUCTION

The problems for salmonids overwintering in ice-covered streams have been recognized for many years (Hubbs and Trautman 1935, Maciolek and Needham 1952, Benson 1955, Logan 1963). The objectives of this report are to summarize what is known about the winter habitats in ice-covered areas for four species of salmonids (Atlantic salmon, brook trout, brown trout and rainbow trout) and to identify the documented effects of winter ice conditions on the developmental stages of Atlantic salmon and trout. An extensive literature search yielded some winter habitat information on the focal velocities, flow depths and substrate types for these species. The data will be presented for each developmental stage for each species.

PHYSICAL MEASUREMENTS OF FISH HABITATS IN ICE-COVERED RIVERS

There have been relatively few fish habitat studies in winter environments where the physical, chemical and biological processes were documented in an ice-covered river. With the development of stable and accurate instruments, in-situ measurements of variables such as flow velocity and depth, water temperature, dissolved oxygen and pH can provide continuous data so that the physical processes in the winter habitat can be understood in more detail. Radio telemetry instrumentation for fisheries research is very advanced, and tracking sensors for very small fish (< 15 cm long) should be available within 2-3 years.

In the fisheries literature the type and distribution of the ice cover throughout the winter were not usually reported or related to winter habitat. In fact, the location of the open water zones (leads) within the ice cover, which may be more significant than where the ice exists, apparently haven't even been addressed. The thermal regime of the river-bed where the eggs and certain juvenile fish reside plays an important role in their development and well-being, and this aspect has not been fully explored.

The physical variables associated with the winter river environment, such as ice thickness and distribution, flow velocity, flow depth and water temperature, have been routinely measured in many hydraulic studies, but the measurement techniques have not been used effectively by aquatic biologists working in ice-covered rivers. In addition, recent studies of river ice processes have shown that previous interpretations of some ice-related factors are not valid, especially those dealing with frazil and anchor ice.

Water temperature

In nearly all streams with a floating ice cover, the water temperature will be close to its freezing point (32°F), providing there are no significant local "warm" inflow sources, such as springs or groundwater upwelling in the immediate area. The water temperature stays close to the freezing point because the ice cover either grows or melts in response to the heat sources acting upon it. Because of turbulence, there is no measurable vertical thermal stratification of the water in steep shallow streams, but a temperature gradient will be detectable in the bed. If the ice cover is rapidly melting,

"warm" water will exist for a short distance beneath it, depending on the velocity, depth, roughness of the ice, etc.

The winter water temperature data reported in the literature have to be evaluated with regard to the physical conditions of the river and the ice regime. Water temperatures higher than 0.2–0.3°C with a floating stationary ice cover indicate that the cover could be melting rapidly at that location, e.g. 3–5 cm/day if the air temperatures are near or greater than 0°C.

Winter water temperatures in gravel streambeds can remain above the freezing point due to groundwater inflow (Hansen 1975); however, local hydraulic, ice and meteorologic conditions can cause portions of the bed to freeze (Calkins and Brockett 1988). Measurements of water temperatures in chinook salmon redds in the Nechako River in British Columbia showed thermal stratification with depth and time-variant temperature profiles, and the dewatered redds showed a deep frost penetration.*

My recent temperature measurements in the substrate of the West Branch of the White River in an open water lead between two floating ice sheets showed subcooled water that entered the gravels could persist for up to 10 hours, generally at night in the absence of solar radiation. Another measurement site in a streambed packed with fine substrate materials showed no indications of subcooling during freeze-up.

Flow depth and ice thickness

When an ice cover forms, remains stationary and floats freely on the water surface, the additional resistance of the bottom of the ice cover will cause the flow depth (measured from the bottom of the ice to the riverbed) to increase compared to the flow depth when no cover was present for the same discharge. The increase in flow depth is related to the ice cover roughness and the type of hydraulic flow regime at the site. For example, the formation of an ice cover can be expected to increase the flow depth by 33% if the ice cover roughness is the same as that of the riverbed, the discharge remains the same and the hydraulic flow conditions are still "uniform."

The total river stage with an ice cover present is equal to the displacement thickness caused by the floating ice (0.92 times the ice thickness) plus the flow depth. The water level stage with a floating ice

cover can be calculated from the hydraulic section properties, the flow discharge, the roughness characteristics of the bed and the under-ice surface, and the ice cover thickness. No fisheries article that I reviewed ever mentioned this fact, and very few data were reported on winter flow regimes beneath ice covers.

In small, shallow and narrow streams, floating ice covers sometimes eventually become nonfloating covers when they become supported by the boulders or banks, and air gaps develop between the bottom of the solid ice and the water surface (Calkins and Brockett 1988). In high-elevation streams with significant snow accumulations, snow can bridge across the streams; in this case the flow depths are not influenced by the ice cover and "open water" conditions prevail under the ice.

In small streams the quantities of ice formed from the various ice processes are significantly different than in larger streams. For example, in some steep mountain streams the ice cover may initially be formed from anchor ice deposits that may not float to the surface because they are attached to the riverbed. These deposits often extend to the water surface and stay in place because the buoyancy force is exceeded as the water level drops, and the solid ice sheet forms from this accumulation. A more detailed description of the various river ice processes can be found in Ashton (1986).

The ice can have some portions solid while a majority could be composed of "slush," a mixture of ice crystals and trapped water in a river; this combination can occupy up to 60–80% of the cross section that is below the water level. After the river is fully covered, the ice conditions change with time: the solid ice sheet grows into the slush ice and some of the slush may melt.

Actual ice thickness measurements and flow depths in habitat areas used by the salmonids investigated in this study are rare. Chisholm et al. (1987) provided some longitudinal data on ice thickness in a small mountain stream in Wyoming.

The ice thickness is usually measured using an auger (hand- or gas-driven) to cut a hole in the ice and a probe (wood, metal rod, wire and rod, etc.) to measure the solid ice thickness. A number of velocity probes are available to measure the flow below the ice once a hole has been drilled. The USGS and CRREL have evaluated several types of velocity meters. The thickness of the slush ice in large rivers is usually determined indirectly from flow velocity measurements; for example, the interface between the flowing water and the slush ice is determined from the vertical velocity profile measurements. In streams less than 1 m deep, slush ice thicknesses may be measured by graduated rods.

* Personal communication with S. Blachut, Department of Fisheries and Oceans, Vancouver.

A new promising method of determining solid and slush ice thicknesses in the larger streams is high-frequency radar pulled by hand over the ice or flown from helicopter (Arcone and Delaney 1987). This technique also identifies when ice is in contact with the substrate as well.

WINTER HABITAT FEATURES OF THE FOUR SPECIES

Table 1 and the sections below summarize information from the literature on winter habitats in ice-covered streams for the four species of salmonid. Many studies have been conducted on winter habitats in rivers and streams without ice covers, but that is not the focus of this report.

Rainbow trout

Eggs and embryos

Rainbow trout are generally spring spawners, and winter habitat does not appear to be a major limiting condition for the survival of eggs and embryos unless the water chemistry changes during the winter or snowmelt period and this somehow affects the redds. Eggs have remained viable when the water temperature was between 0.3° and 2.0°C (Raleigh et al. 1984).

Fry

I found no studies focusing on overwintering fry habitat in ice-covered rivers; however, many authors including, Hartman (1965) and Bustard and Narver 1975, studied fry in winter streams without

Table 1. Habitat features of Atlantic salmon, brook trout, brown trout and rainbow trout in the presence of an ice cover.

	<i>Focal depth (cm)</i>	<i>Focal velocity (cm/s)</i>	<i>Substrate (cm)</i>	<i>Reference</i>
Atlantic salmon				
Eggs/embryos*	15-75	25-90	gravel redds (autumnal conditions)	Beland et al. (1982)
Young-of-year	45-49	41-46	rubble gravels	Cunjak (1988)
Juveniles	41	39	rubble gravels	Cunjak (1988)
Brook trout				
Eggs/embryos*			0.3-5	Reiser & Wesche (1979)
Fry	27-40	0.5-4.3	10-40	Cunjak & Power (1986)
Juveniles/adults	40-95	4.6-17.8	—	Cunjak & Power (1986)
Adults	—	<15	sand/silt	Chisholm et al. (1987)
Brown trout				
Eggs/embryos*	>9	15-46	gravel	Reiser & Wesche (1977)
Fry	43-46	2.2-4.7	boulders to sand	Cunjak & Power (1986)
Juveniles/adults	50-75	5.7-16	boulders to sand	Cunjak & Power (1986)
Rainbow trout				
Juveniles	—	—	gravels	Everest (1969)
Adults	—	—	gravels	Chapman & Bjornn (1969) and several authors

*Spawning conditions.

ice. Johnson and Kucera (1985) also reported on fry transition from summer to autumn habitats. The biggest change was that a majority of the fish moved toward larger substrates from the gravels where the mean flow velocity over the larger material was less than 20 cm/s, the same conclusions reached by others.

Juveniles

Log jams, rubble, upturned roots and debris piles appear to be important sources of winter cover (Bustard and Narver 1975a, Wesche 1980); these are also sources of summer cover. Everest (1969) found that during the freeze-up period, juvenile rainbow trout were 15–30 cm deep in the gravels, which were often covered by 5–10 cm of anchor ice.

Adults

Adult trout overwinter in larger streams and flat water areas with abundant hiding places. The principal cover is associated with boulders in main-stream areas (Chapman and Bjornn 1969). Trout activity is apparently reduced in winter, and adults remain in one place during this time (Chapman and Bjornn 1969). Raleigh et al. (1984) reported that only 6 cm of water depth was required for travel.

Brook trout

Eggs and embryos

Brook trout are fall spawners, and the eggs that are deposited in the gravels are susceptible to ice effects in streams where ice covers form. The dissolved oxygen content should not fall below 50% saturation in the redd for embryo development to occur (Harshbarger 1975). Reiser and Wesche (1977) contend that the optimum substrate size for brook trout embryos ranges from 0.3 to 5.05 cm. The optimum spawning gravel should contain 5% or less of fines and include gravel ranging from 3 to 18 cm in diameter (Raleigh 1982).

Fry

Fry emerge from gravel redds after the ice cover has disappeared (if the stream freezes over). This may range from January to April, depending on water temperature (Brasch et al. 1958). Raleigh (1982) reported that upwelling groundwater areas are an important consideration for the well-being of fry.

Cunjak and Power (1986) reported that the mean focal point velocities occupied by fry were between 1.5 and 4.3 cm/s, and the mean focal-point depths ranged from 27.6 to 40.3 cm. From 79.6 to 100% of

the fry observed underwater were associated with cover. Cunjak and Power's information on the depths under the ice cover is restricted to near the shore ice edge; they sampled only two sites, which had between 22 and 24% of the stream surface area covered with ice. The open water lead would control the flow depths and velocities because the shore ice does not extend far enough into the stream to alter the flow regime.

Juveniles and adults

Cunjak and Power (1986) reported juveniles in winter occupying mean focal point depths from 42.4 to 95.4 cm and mean focal point water velocities from 4.6 to 17.8 cm/s. The surface ice coverage was the same as for the fry. Juvenile brook trout appear to associate more with substrate cover than with overhead streambank cover (Wesche 1980). Cunjak and Power (1986) also reported that 83.3–91.4% of the over-yearlings were associated with substrate cover in winter; at all sites the percentage found in substrate cover was higher in winter than in summer.

Cunjak and Power (1986) concluded that trout older than 1 year were able to withstand higher velocities and greater depths than the fry. They did not observe trout hiding in the substrate in the winter in the Credit River, although this has been observed in streams with a more severe ice regime. Adults require an oxygen concentration near saturation; 7 mg/L or greater is required at temperatures below 15°C (Raleigh 1982). Water velocities between 7 and 11 cm/s are preferred during the summer, with a maximum velocity of 25 cm/s (Griffith 1972). Cunjak and Power (1986) found that adults occupied winter depths between 42.4 and 95.4 cm or greater and focal velocities between 4.3 and 17.8 cm/s. Chisholm et al. (1987) found that adult trout preferred velocities below 15 cm/s, relatively deep water, and a sand-silt substrate over 80% of the time. Cunjak and Power (1986) reported that the range in substrate composition occupied by brook trout in their study areas was 3–5% boulders, 8–20% rubble, 10–23% gravel, 29–43% sand, 4–14% silt, and 2–5% logs, with 0–34% macrophytes and algae on the substrate.

Brown trout

Eggs

Brown trout are also fall spawners, and eggs are deposited up to 20 cm into a gravel substrate. If an ice cover is present, then the stream water temperatures will reach 0.0°C. Redds may be located at the downstream end of a pool that merges into a riffle

area, where the water flow is fairly fast and the water depth is moderate (Stewart 1953). Females avoid spawning in areas of undiluted groundwater discharge or low oxygen concentration, and they select sites that contain an intersurface groundwater mix with sufficient oxygen (Hansen 1975). In-flowing groundwater minimizes fluctuations in water level and temperature (Cunjak and Power 1986), creating redd conditions that are conducive to early hatching (Hansen 1975). The average water depth and velocity over the redds are 9 cm and 15–46 cm/s, respectively (Reiser and Wesche 1979). The redd temperature does not greatly influence the survival of eggs (Hansen 1975), as the survival of eggs in redds with a temperature of 0–1°C was only slightly higher than in warmer redds; however, eggs survived at all observed redd temperatures between 0° and 8°C.

Fry

Cunjak and Power (1986) did extensive research on the winter habitat of brown trout fry in the Credit River in central Ontario, although the ice cover conditions were minimal to moderate during the study period. The material cited below comes from their work.

Fry utilized shallow, low-velocity reaches and spring-fed tributaries with abundant cover. Fry were never found overwintering beneath rocks. The composition of the substrate in which fry were located consisted of 43% boulders, 28% rubble, 14% gravel, 1% silt, 0% logs, and 1% macrophytes and algae on the substrate.

The mean focal point depth occupied by fry in the winter was nearly the same as during the summer, ranging from 43.1 to 46.2 cm. The importance of the depth occupied by fry may be in providing cover and protection from the current. Mean focal point velocities ranged from 2.2 to 4.7 cm/s in winter, while the summer value was reported to be 13.6 cm/s. All fry occupied positions beneath cover.

The winter conditions of the streams where brown trout were located generally consisted of areas of groundwater inflow with no or limited ice formation.

Juveniles and adults

Cunjak and Power (1986) also documented the winter habitats of juvenile and adult brown trout. The information cited below is from their work.

The composition of the substrate in which juvenile brown trout were observed was the same as for fry. The winter water temperature range of the streams in which brown trout were observed was

also the same as the fry: 0.1–1.5°C. The dissolved oxygen concentration was near saturation, with trout associating with cover often in areas near groundwater sources. From 88.9 to 100% of the fish were associated with some form of cover. The trout were generally in deeper, slower water (ranging from 5.7 to 16.0 cm/s) with greater overhead cover in winter than in summer.

Hartman (1963) contends that trout associate with cover and shade in regions of low water velocities while remaining in one location in winter.

Atlantic salmon

Eggs

The measured depth of egg deposition in 38 redds in Maine rivers, documented by the Atlantic Sea-Run Salmon Commission (1981), ranged between 10 and 23 cm. The average size of the redds was 3.8 m². Permeability in the redds, standardized to 10°C, as measured in Maine rivers using the standard technique described by Terhune (1958) ranged from 74 to 4680 cm/hr, with permeabilities of 2500–4680 cm/hr found at sites where the redds had been used more than one season (Atlantic Sea-Run Salmon Commission 1981). LaCroix (1985) measured the permeability of natural redds in Nova Scotia using the same method and came up with values of 153–22,320 cm/hr, with an average of about 4000 cm/hr; these are similar to the values reported for the redds in the Maine rivers. LaCroix (1985) concluded that low values of either pH and dissolved oxygen did affect egg survival in some western Nova Scotia streams.

Extensive observations of overwintering eggs in severe ice areas, such as the small streams in New England where fry and parr are being released, have not been conducted.

Fry

The fry of Atlantic salmon in New England and the Atlantic provinces emerge from the gravels in May and June (Gustafson-Marjanen and Dowse 1983, LaCroix 1985), but precise dates depend on the physical and chemical conditions in the river during this period.

The location of fry during the winter in ice-covered New Brunswick rivers appears to be the same as during the summer, except that they are hiding in the water between the bed materials (Rimmer et al. 1983, 1984). However, Saunders and Gee (1964) reported that the fry were hiding under streambanks, around large rocks and under boulders during late December before the ice cover had formed. The most common habitat features for fry

during the summer were riffles, shallow depths and small stones of 2–6 cm diameter.

There was no direct evidence that the ice cover limits the fry habitat. Many researchers have inferred that frozen gravels caused by severe winters, ice-covered riffles (preventing the interchange of flow into the gravel), and low winter flows are all possible limiting factors, but no one has reported any direct measurements. Gibson and Meyers (1988), Chadwick (1982), Walsh and Calkins (1986) discussed these possible winter limiting factors and their impact on available Atlantic salmon habitat.

Parr

As documented for the fry, Rimmer et al. (1983, 1984) found that the 1+ and 2+ parr also stayed in their summer habitat during autumn and moved into the substrate as the water temperature started to drop below 10°C. The summer flow depths and home stones preferred by parr increased as the body size increased. Rimmer et al. (1983) reported some movement of the different age classes in the autumn from their summer habitat, but it was an insignificant number of fish compared to the total population.

Cunjak (1988), documenting the microhabitat of young salmon in the winter, found that they were consistently hiding beneath rocks (17–23 cm in diameter) in riffle-run habitats. They also used the stones associated with the main flow area instead of the streambank zones.

Again, no direct evidence of ice cover influence on the survival of the parr can be found in the literature, although the same inferences mentioned for the fry may also be true for parr. For example, cold winters combined with low flows may increase the mortality (Gibson and Meyers 1988).

Adults

The winter habitat of returning sea salmon has not been documented extensively in the open literature. According to Danie et al. (1984) the kelts remain in the freshwater streams, presumably in the deeper pools, or they return to the estuaries. There appears to be little known about the winter life cycle after spawning.

DISCUSSION

The first year of life for the Atlantic salmon is the most sensitive to environmental influence (Chadwick 1982). From a survey of existing literature it appears that early developmental stages of trout

and salmon favor areas of gravel, sand and rubble located in shallow areas of low velocity with near saturation of dissolved oxygen. The winter habitat selected by trout may be based on the theory of energetic cost minimization, which contends that trout choose stream positions that afford them access to food, while requiring them to expend the least amount of energy. Winter environmental occurrences such as anchor ice, sheet ice and snow-melt all cause wide fluctuations in water levels, which are detrimental to stable habitat. Low survival of egg and fry populations in Newfoundland rivers occurred during cold winters with low river discharge preceded by high discharge during spawning (Chadwick 1982). A low river flow could expose a greater portion of the redds, the low temperatures could mean a greater frost penetration into the redds, and the high spring flows could move the substrate; all of these are detrimental to overwintering salmon. Spawning in redds when the discharge is above normal in the fall and when the stages drop during the winter subjects more eggs to exposure and freezing (Chadwick 1982).

LaCroix (1985) reported that eggs are vulnerable to seasonal or episodic changes in the quality of water, and successful hatching is highly correlated with mean pH. Acid precipitation appears to have eliminated the stocks of salmon in eight to ten rivers in Nova Scotia (Gourlay 1980). A pH value of 4.5 or lower is lethal to developing salmon (Peterson et al. 1980). Midwinter runoff events induced by rain on snow may be as significant as spring runoff in releasing hydrogen ions in the snowpack.

The duration of near-freezing water temperatures at which both the young and older members of a population survive appears to vary from river to river (Jensen and Johansen 1986). This suggests that fish populations genetically adapt to their rearing environment, and if this is the case, the question becomes, How well do these populations adapt and what are the limits of this adaptation? Riddell and Leggett (1981) reported that population variability, morphology and downstream migration are adaptations to the rearing environment. Saunders (1980) contends that genetic control is likely for triggering smolting and migration behavior and that the gene pool adapts to the local environment. Therefore, it is plausible that the duration of low water temperatures that trout and salmon can withstand are likewise genetic adaptations.

Anchor ice may affect the survival of trout eggs, fry and juveniles in many ways by attaching to the spawning redds and the stream bottom. First, the anchor ice can cut off the flow of water into the redd

or gravels, denying them adequate water quality. Second, prolonged anchor ice conditions may accelerate growth of solid ice into the redds (Walsh and Calkins 1986). During freeze-up, water is held in storage, and the stream stage rises. The anchor ice attaches to rocks, often blocking the flow and diverting it to the side channels, making the water levels rise. Consequently fish that moved into the side channels during the stage rise can be stranded when the water level and ice cover drop (Maciolek and Needham 1952). Deposition and melting of anchor ice in daily cycles causes the river stage to rise and fall, and during the decline, stream bottom scouring is possible. Benson (1955) and I have observed trout spawning in riffles where anchor ice forms.

Sheet ice has been known to damage the stream edge during break-up. This could be disastrous for brown trout, which appear to prefer the stream edge (Maciolek and Needham 1952). Ice break-up and the associated ice runs in streams induce strong transient flow velocities (> 5 m/s), and during this period significant bed movement occurs, as well as scour at the shoreline.

Snowmelt and floods affect trout populations, depending on the timing of the melt and the spawning period of the trout (Seegrist and Gard 1972). When brook and brown trout eggs are devastated by winter floods, rainbow trout populations rise; conversely, when rainbow trout eggs are devastated by spring floods, a rise in the brook and brown trout populations can be anticipated (Seegrist and Gard 1972).

CONCLUSIONS

In the last ten years researchers have begun to focus specifically on the winter habitat requirements of salmonid species. Measurements of the habitat features are slowly being published, so winter profiles for the different species are beginning to show some trends. Focal point velocities and flow depths for the fry of brook trout, brown trout and Atlantic salmon are all less than 10 cm/s and 40 cm, respectively. Juveniles of these species prefer focal velocities less than 15 cm/s.

The river ice conditions (ice type and thickness, water depths, flow velocities, open water areas, etc.) as they develop and change during the winter have not been thoroughly documented for the different habitat reaches. Many studies have focused on the period just prior to freeze-up, but only a few actually continued the observations throughout the winter.

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